Dicranum ignatovii sp. nova (Dicranaceae, Bryophyta) from the Far East

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ABSTRACT

The new species *Dicranum ignatovii* Tubanova & Fedosov is described from Sakhalin, South Kurile Islands and the Khabarovsk Territory based on the approach of integrative taxonomy. The species is characterized by the unique combination of (1) short leaves with broadly acute apex, (2) slightly recurved distal leaf lamina, (3) short-rectangular to transverse rectangular distal leaf cells, (4) proximal leaf cells abruptly shortened distally and thus occupying only the basalmost leaf portion, (5) costa ending before apex, and (6) presence of flagelliform branchlets in upper leaf axils. Based on nrITS 1, 2 & 5.8 rRNA gene sequences, molecular phylogenetic analysis was carried out. As a result, three studied specimens were found in a well supported clade, nested in a weakly supported clade where *D. acutifolium, D. caesium, D. bardunovii, D. angustum, D. bonjeanii, D. scoparium* and *D. brevifolium* were also found.

INTRODUCTION

For the first time, an unusual corticolous specimen of *Dicranum* Hedw. was collected by Mikhail S. Ignatov, who carried out extensive bryofloristic exploration of Kunashir Island. That specimen combined such specific traits as distally keeled leaves, slightly recurved leaf margins, rectangular to transverse-rectangular distal leaf cells, and rather sharp transition from proximal to distal leaf cells. Combination of these traits is unique within the genus and made this specimen quite distinctive from other species of *Dicranum*. Since the ITS sequence obtained from this specimen did not attribute it to any of the known species, it has been kept until more collections were available. Further field works in Iturup and Sakhalin Islands along with revision of the *Dicranum* specimens from VGBI and the Herbarium of the Institute of Marine Geology and Geophysics FEB RAS (IMGG FEB RAS) revealed additional specimens with the same combination of morphological traits. Nevertheless some of these specimens had flagelliform branchlets arising in the upper leaf axils. This trait occurs in a few species of the genus *Dicranum*, mostly belonging to the subgenus *Orthodicranum* Bruch & Schimp., namely *D. flagellare* Hedw., *D. montanum* Hedw., and *D. mayrii* Broth. One more species, *D. leoneuron* (subgenus *Dicranum* Schimp.), also possesses flagelliform branchlets being distinguished by this feature from the closely related *D. bonjeanii* De Not. Morphologically all aforementioned species are clearly different from the revealed specimens.

Though the combination of revealed traits is unique within the genus and distinctive enough to refer a few collected specimens to a new species, variation within the known species is still poorly examined; in addition, affinity of our specimens within the genus *Dicranum* is not clear. Thus we decided to test its status and identify its affinity using the molecular phylogenetic approach.

MATERIAL AND METHODS

Nuclear ITS1,2 & 5.8 rRNA gene region was used for the molecular phylogenetic study, because it provides stronger phylogenetic signal comparing to chloroplast markers; variation of the latter is not enough to resolve the phylogeny within large subclades of the genus. This marker was successfully used in similar studies that focused on the genus (Ignatova & Fedosov, 2008; Tubanova *et al.*, 2010; Tubanova & Ignatova, 2011; Ignatova *et al.*, 2015; Tubanova *et al.*, 2016). Laboratory protocol was essentially the same as it was reported in previous moss studies and described in detail e.g., Gardiner *et al.* (2005). The newly obtained sequences were added to the alignment produced during *Dicranum* molecular phylogenetic studies (available

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from author upon request). As a result of testing phylogenetic reconstructions, the set of species to be involved in the final reconstruction as the most closely related lineages was determined. The suite of species being classified in sect. *Orthodicranum* has been included into analysis since our target specimens resemble them in having flagelliform branchlets. The latter trait is quite unusual among other infrageneric groupings of *Dicranum*. In total, 61 specimens related to 22 *Dicranum* species were involved in the analysis including 26 sequences obtained *de-novo* - the target taxon was represented by three sequences obtained from different specimens (Appendix 1). Two sequences of *Paraleucobryum longifolium* (Ehrh. ex Hedw.) Loeske were obtained and involved as an outgroup, since this species was found to be the most closely related to *Dicranum* (Stech *et al.*, 2012); other tested outgroups were hard to align with the compiled *Dicranum* dataset due to ambiguous homology. Sequences were aligned using MUSCLE (Edgar, 2004) and subsequently manually edited in BioEdit version 7.0.9.0 (Hall, 1999). Absent positions at 3' & 5'-ends were treated as missing data. The alignment comprised 863 positions, corresponding to ITS1 (1^{st} -356^{th} positions), 5.8S rRNA gene (357^{th} -513^{th} positions) and ITS2 (514^{th}-836^{th} positions), considered as unlinked partitions. Trees were rooted on *Paraleucobryum longifolium*.

Best-fit substitution models were identified for each partition separately and for whole dataset using Partitionfinder V1.1.1 (Lanfear *et al.*, 2012). Best-scoring Maximum Likelihood (ML) tree was estimated using RaxML (Stamatakis, 2006) from 100 independent searches, each starting from a distinct random tree. Robustness of the nodes was assessed using the thorough bootstrapping algorithm (Felsenstein, 1985) with 1,000 iterations. Bayesian analysis (BA) was performed running two parallel analyses, each run consisted of six Markov chains and 25,000,000 generations with default number of swaps chains in MrBayes 3.2.6 (Ronquist *et al.*, 2012). Convergence of each analysis was evaluated using Tracer1.4.1 (Rambaut & Drummond, 2007) to check that all ESS values exceeded 200. Consensus tree was calculated after the first 25% trees were discarded as burn-in.

Results

In the phylogenetic reconstruction obtained from ITS sequences (Fig. 1) the genus *Dicranum* forms a highly supported clade with the clade of *D. viride* (Sull. & Lesq.) Lindb. resolved as a sister to the rest of the genus. The next node represents polytomy, which comprises (1) a highly supported *D. mayrii* clade (PP=1, BS=100), (2) a moderately supported "*Orthodicranum*-clade" (*D. flagellare* plus *D. montanum*, PP=1, BS=87), and (3) an unsupported polytomy, including other considered species of the genus *Dicranum*. In

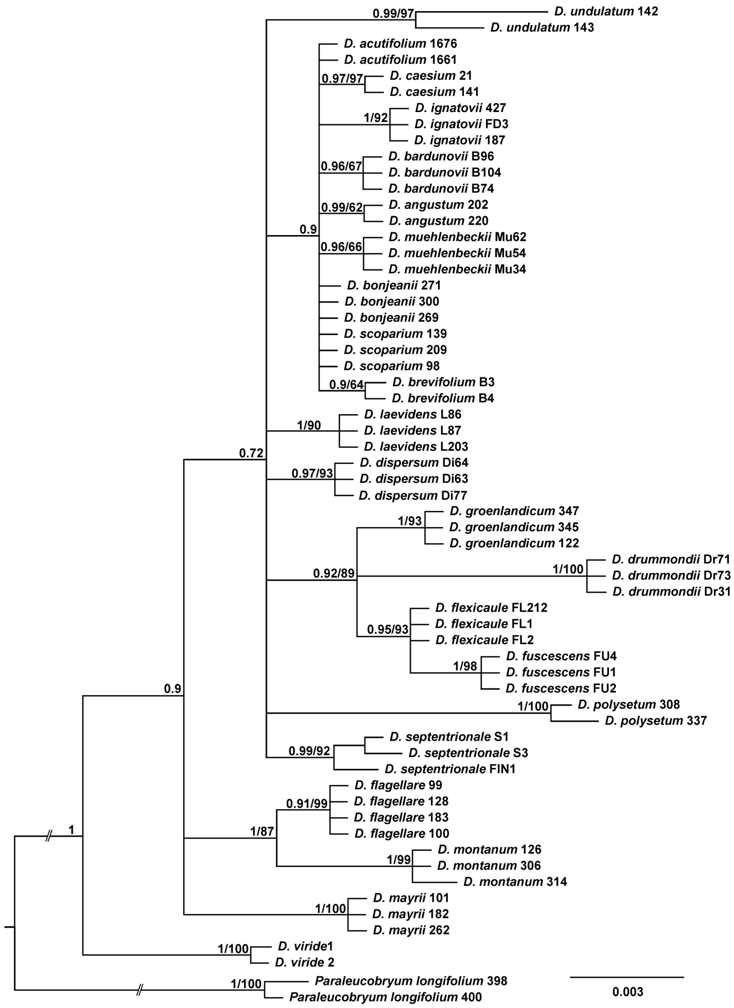

Figure 1. Bayesian tree obtained from ITS sequences. Posterior probabilities (>70) / BS support (>50) from the best RAxML likelihood tree (if applicable) are indicated.

this polytomy two weakly supported polyspecific clades and five moderately to highly supported unispecific clades, corresponding to (1) *D. septentrionale* Tubanova & Ignatova (PP=0.99, BS=92), (2) *D. polysetum* Brid. (PP=1, BS=100), (3) *D. dispersum* Engelmark (PP=0.97, BS=93), (4) *D. laevidens* Williams (PP=1, BS=90), and (5) *D. undulatum* Schrad. ex Brid. (PP=0.99, BS=97) are nested. The first of two polyspecific clades comprises subclades of *D. groenlandicum* Brid. (PP=1, BS=93), *D. drummondii* Müll. Hal. (PP=1, BS=100) and *D. flexicaule* Brid. plus *D. fuscescens* Sm. (PP=0.95, BS=93). The second polyspecific clade represents a weakly supported polytomy, where some nested unispecific subclades are nested along with specimens of *D. acutifolium* (Lindb. & Arnell) C.E.O. Jensen, *D. bonjeanii*, and *D. scoparium* Hedw., which do not form further groupings. Among the nested unispecific clades, corresponding to *D. caesium* Mitt. (PP=0.97, BS=97), *D. bardunovii* Tubanova & Ignatova (PP=0.96, BS=97), *D. angustum* Lindb. (PP=0.99, BS=62), *D. muehlenbeckii* Bruch

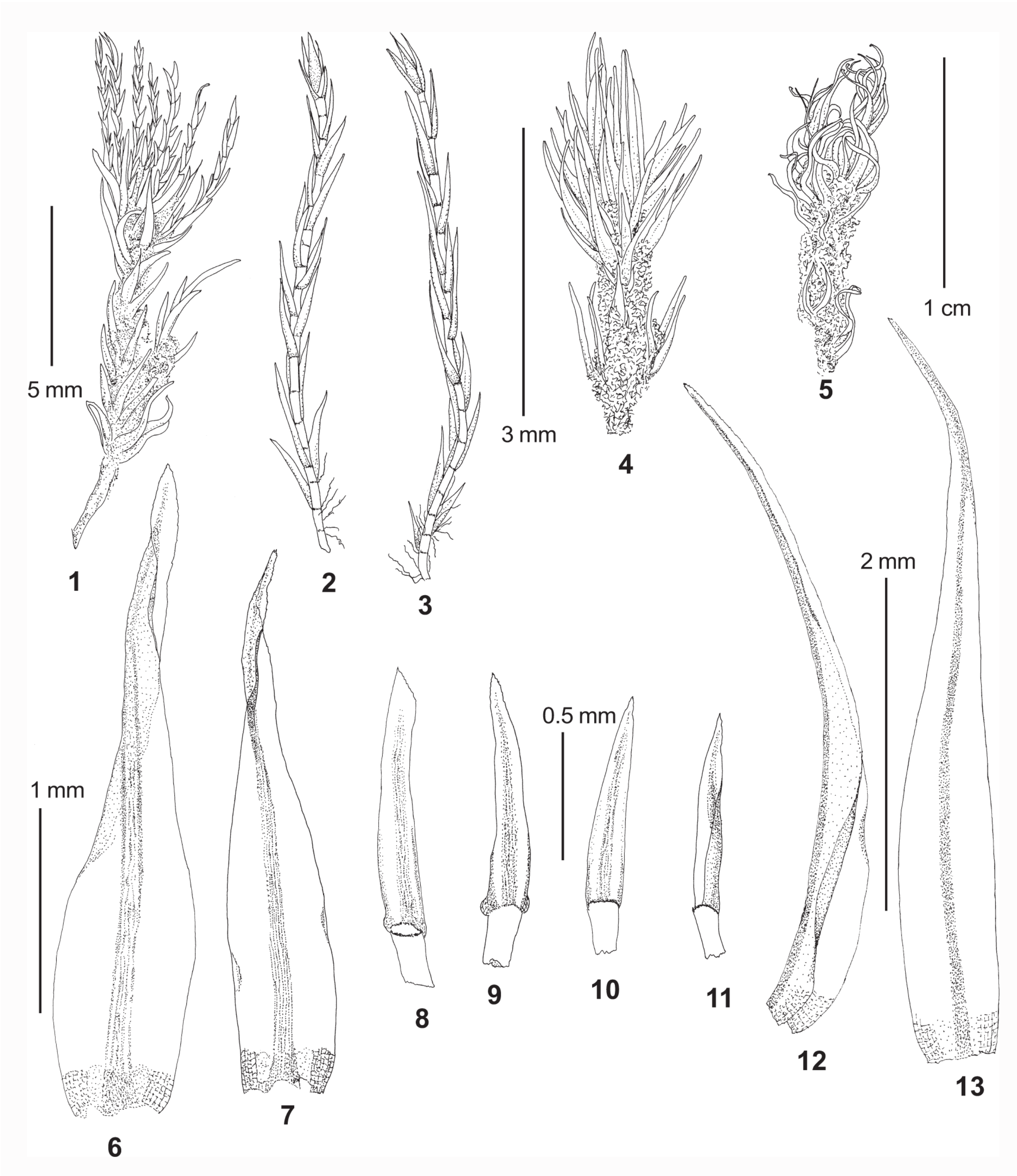

Figure 2. *Dicranum ignatovii* (1–3, 6–11 from: Iturup Island, Vicinity of Cirk Bay, 11.IX.2015, Fedosov # 15-2-123, MW; 4–5, 12–13 from: Holotype, UUH. 1 – habit with the flagelliform branchlets, wet; 2–3 – flagelliform branchlet; 4 – habit, wet; 5 – habit, dry; 6–7, 12–13 – leaves; 8–11 – flagellum. Scale bars: 5 mm for 1; 3 mm for 2–3; 1 cm for 4–5; 1 mm for 6–7; 0.5 mm for 8–11; 2 mm for 12–13.

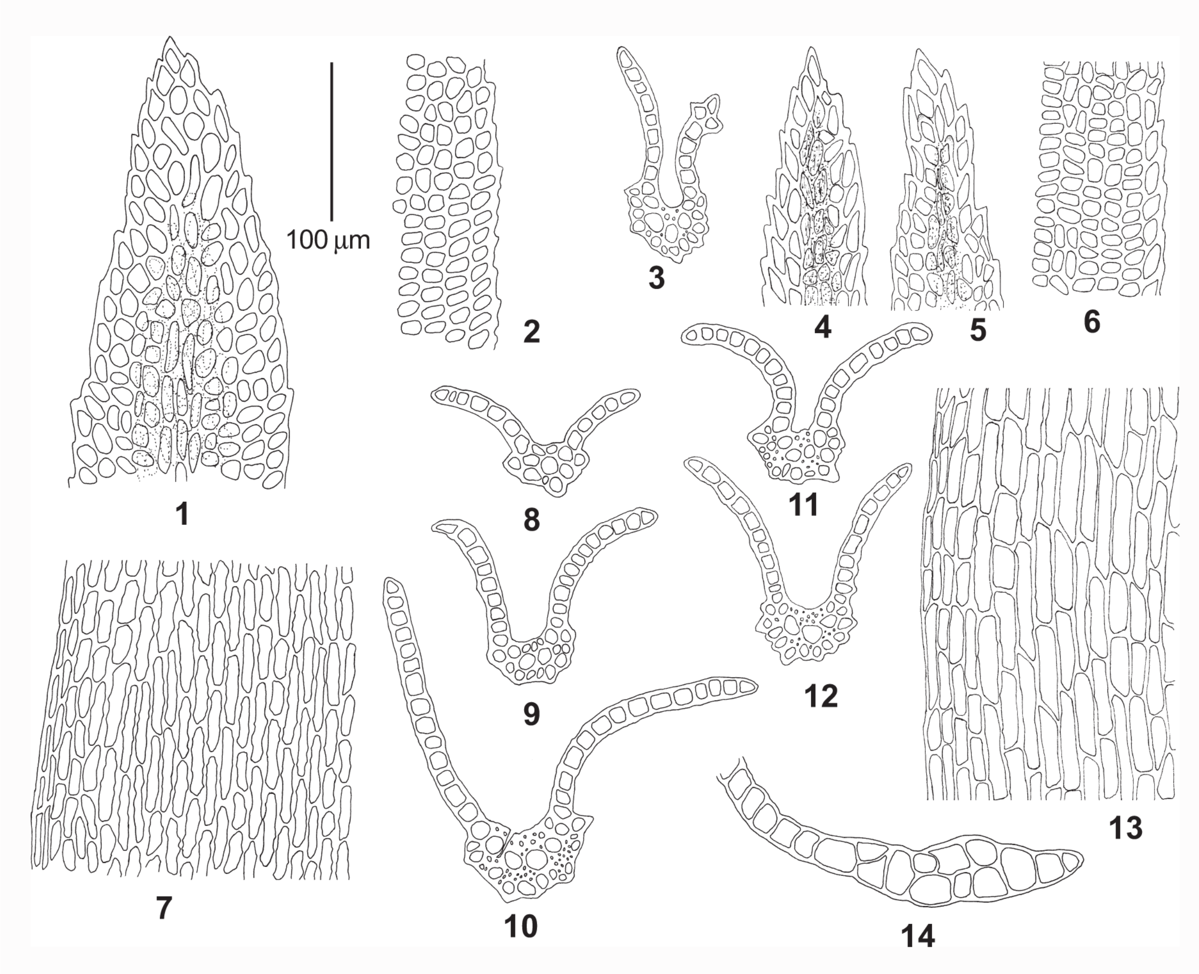

Figure 3. *Dicranum ignatovii* (1–2, 7–10 from: Iturup Island, Vicinity of Cirk Bay, 11.IX.2015, Fedosov # 15-2-123, [MW]; 3–6, 12–14 from: Holotype, UUH. 1, 4–5 – leaf apical part; 2, 6 – upper leaf cells; 3, 8–12 – leaf transverse sections; 7, 13 – basal leaf cells; 14 – alar cells transverse sections. Scale bars: 100 µm for 1–14.

& Schimp. (PP=0.96, BS=66), and *D. brevifolium* (Lindb.) Lindb. (PP=0.90, BS=64), the target specimens form a separate highly supported clade (PP=1, BS=92). Thus, the unique combination of morphological characters in revealed specimens is supported by molecular data and on this basis he material is described as a new species below.

Taxonomy

Dicranum ignatovii Tubanova & Fedosov, sp. nov. Figs. 2-3.

Type: Russian Far East, Sakhalin Region, Kurile Islands, Kunashir, 2 km N of Yuzhno-Kurilsk Town, 44°03' N, 145°61' E, ca. 10 m a.s.l., spruce forest of *Picea glehnii*, on spruce trunk, 9.IX.2006, coll. M.S. Ignatov # 06-3008 [holotype UUH!, isotype MHA!]

Diagnosis. The species is similar to *D. undulatum* in having blunt leaf apices, costae ending below leaf apices and lacking ventral epidermis, but differs from it in smaller size, corticolous growth, numerous flagellae and short, mostly transverse rectangular upper leaf cells. Among other traits of the species leaf margins, which often are slightly recurved and uneven, often angulate on transverse leaf section costae are to be mentioned.

Etymology. The new species is named in honor of the first collector, Dr. Mikhail S. Ignatov.

Description. Plants in dense compact tufts, light to bright green, not glossy. Stems 1-2.5 cm, moderately to densely tomentose, with whitish tomentum in upper part and reddish brown tomentum at the base, more or less densely foliate. Leaves slightly curved to flexuose when dry, straight or slightly curved when wet, 2.5–4.1(–4.9) mm, from ovate-lanceolate to lanceolate base, gradually narrowed to broadly acute, rarely narrowly acute apex, distinctly keeled distally; margins plane, or slightly recurved distally, serrate distally, unistratose, occasionally bistratose distally; costa strong, strongly scabrous above on abaxial surface, ending few cells below apex, at base 1/5–1/8 of leaf width, with a row of guide cells, two stereid bands, adaxial epidermal layer of cells not

differentiated, abaxial layer differentiated; lamina 1-stratose, in upper part, smooth or slightly prorate on distal abaxial surface; distal lamina cells (6–)9–13(–18)×(6–)11–15(–19) µm, subquadrate, short-rectangular or transverse-rectangular, rarely triangular or irregularly angled, with rounded corners and evenly thickened walls, not porose; proximal lamina cells (17–)35–61(–88.5)×(6–)9–12(–14.7) µm, short rectangular to linear, weakly incrassate, porose, abruptly shortened distally in middle leaf part; alar cells light brownish 1-2-stratose, not reaching the costa. Vegetative reproduction by flagelliform branchlets up to 5 mm height that arise in upper leaf axils; leaves of flagelliform branchlets are small, 0.5-1 mm, ovate-lanceolate, broadly acute, slightly serrate, breaking off with branch pieces. Sporophytes and male plants were not seen.

Other specimens examined. Sakhalin Region: (1) Sakhalin Island, vicinity of Yuzhno-Sakhalinsk town, Susunaisky Ridge, Bolshevik Mt., (46°57'09.9"N, 142°47'43.4"E), ca. 564 m a.s.l., spruce & fern dominating forest with admixture of birch and rowan, on spruce trunk, 20.VII.2015, coll. D. Tubanova, O. Tumurova, L. Dorzhieva # S14015/17 [UUH]; (2) Iturup Island, Vicinity of Cirk Bay (45,32 N°, 148,61°E), ca. 48 m a.s.l., in open *Betula ermanii* stand with *Sasa* on steep rocky slope; on birch trunk, 11.IX.2015, coll. V. Fedosov # 15-2-123 [MW]; (3) Kunashir Island: Mendeleev volcano, north-west slope (43˚59'46"N, 145˚43'18"E), ca. 270 m a.s.l., in *Picea glehnii* [admixtured with fir – note by D.T.] forest with *Sasa*, on fir trunk, 10.VIII.2015, coll. T. Koroteeva # 15-20/3-10 [Herbarium of IMGG FEB RAS]; vicinity of Lagunnoe Lake, mixed coniferous and broadleaf forest (44˚2'9"N, 145˚ 45'28"E), ca. 140 m a.s.l., on spruce trunk, 15.VIII.2015, coll. T. Koroteeva # 15-12/3-8 [Herbarium of IMGG FEB RAS]; Khabarovsk Territory: Ul'chsky District: (1) 20 km north-east of the De-Castri Village, north part of Tabo Bay, (51°37'55"N, 140°54'5"E), ca. 105 m a.s.l., spruce & fir dominating forest, on birch, 5.VIII.2011, coll. L. Yakovchenko & E. Roenko # Kh-22-5-11 [VBGI]; (2) 23 km north-east of the De-Castri Village, vicinity of Tabo Bay (51°39'7"N, 140°54'53"E), 248 m a.s.l., mixed forest dominated with *Ledum* in the ground layer, on fir bark, 6.VIII.2011, coll. L. Yakovchenko & E. Roenko # Kh-34-1-11 [VBGI].

Differentiation. Among the corticolous *Dicranum* species some have similar but not identical flagelliform branchlets. First of all these are some species of the subgenus *Orthodicranum*, namely *D. flagellare, D. mayrii* and *D. montanum*. *Dicranum ignatovii* differs from them in being bistratose vs unistratose alar group, leaves keeled in upper part, broadly acute at apex vs tubulose, narrowly acute, costa ending before apex vs. percurrent or excurrent in the subgenus *Orthodicranum*. Furthermore, the traits of branchlets are useful to separate these species. In *D. montanum* branchlets are not fragile; in *D. flagellare*, *D. mayrii*, and *D. ignatovii* branchlets are fragile, breaking off with pieces of branches. In *D. montanum* branchlet leaves are narrow, acute, and curly; in *D. flagellare* and *D. mayrii* branchlet leaves are wide, blunt, and tightly cuddled; in *D. ignatovii* branchlet leaves are ovate-lanceolate, broadly acute.

In the genus *Dicranum* s.str. obligatory epiphytes are limited; among them *D. viride* can be ascribed, but cannot be morphologically confused with *D. ignatovii*; in *D. viride,* leaves are tubular and fragile and the costae bear ventral epidermis, while in *D. ignatovii* leaves are keeled and not fragile, and the costa does not bear a ventral epidermis. Nevertheless, some *Dicranum* species occasionally inhabit tree trunks and could be confused with *D. ignatovii*. In blunt leaf apices and costae ending below leaf apices as well as in recurved leaf margins *D. ignatovii* is similar to *D. undulatum*, but it differs from the latter species in its smaller size, growth on tree trunks, transversely extended distal leaf cells and in having flagelliform branchlets.

In shape of distal leaf cells and rather sharp transition between proximal and distal leaf cells *Dicranum ignatovii* resembles *D. brevifolium*, but it differs from the latter species in recurved distal leaf margins (plane in *D. brevifolium*), not bulging longitudinal cell walls and flagellae (never occurring in *D. brevifolium*).

Dicranum leioneuron Kindb. is one of a few *Dicranum* s. str. species, which resembles *D. ignatovii* in having flagelliform branchlets; the latter is readily distinct in corticolous growth, smaller size and subquadrate distal laminal cells vs. growth on soil, larger size and prosenchymatous distal leaf cells in *D. leioneuron*.

Dicranum acutifolium, D. caesium and *D. bardunovii* are closely related to *D. ignatovii* according to the obtained molecular-phylogenetic reconstruction. These species differ from *D. ignatovii* by the (1) elongate proximal leaf cells, which gradually become shorter distally (in *D. ignatovii* this transition is rather sharp); (2) acuminate leaves with percurrent to short excurrent costa (blunt, with costae ending below leaf apex in D. *ignatovii*); and (3) plain or shaped like a pair of tongs in upper part of leaf (recurved in *D. ignatovii*). *Dicranum laevidens* and *D. angustum* have tubular distal leaf lamina, while *D. ignatovii* has keeled, never tubular distal leaf lamina. *Dicranum bonjeanii* and *D. scoparium* have elongate, porose upper leaf cells and emergent cells or low lamina in dorsal surface of costa, which is lacking in *D. ignatovii*.

Distribution and ecology. Based on the studied specimens, *Dicranum ignatovii* grows on birch, spruce and fir trunks in various types of woodlands in lower altitudinal belt, at 100–

Figure 4. Known localities of *D. ignatovii*

500 m a.s.l., in a humid cool temperate and hemiboreal monsoon climate. According to the data on hand, this species occurs in Sakhalin, South Kurile Islands and Khabarovsk Territory (Fig. 4).

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Appendix 1. Specimens used in the analyses, with the GenBank accession numbers. The accessions of newly generated sequences are boldfaced and supplied with the specimen voucher information.

Species	# in tree Isolate	nrITS1-2	Specimen data (for newly generated sequences)
Paraleucobryum longifolium	**398**	**MG214822**	**Russia, Republic of Buryatia, 03.VII.2013, *Tubanova #Ka-01/13* (UUH)**
Paraleucobryum longifolium	**400**	**MG255123**	**Russia, Sakhalin Island, 24.VII.2014, *Tubanova #S-14021* (UUH)**
acutifolium	Dic_1661	KJ650866	Norway
acutifolium	Dic_1676	KJ650879	Norway
angustum	A202	KT580731	Russia, Yamal-Nenets Autonomous Area
angustum	A220	KT580732	Russia, Yamal-Nenets Autonomous Area
bardunovii	B96	JN897272	Russia, Republic of Buryatia
bardunovii	B104	JN897273	Russia, Republic of Sakha (Yakutia)
bardunovii	B74	JN897274	Russia, Republic of Sakha (Yakutia)
bonjeanii	**271**	**MG214796**	**Russia, Murmansk Region, 27.VI.2012, *Ignatov, Ignatova #12-12* (MHA)**
bonjeanii	**300**	**MG214797**	**Russia, Republic of Buryatia, 30.VII.2008, *Tubanova, Anenkhonov #ErT-04/08* (UUH)**
bonjeanii	**269**	**MG214798**	**Russia, Republic of Dagestan, 20.V.2009, *Ignatov, Ignatova #09-699* (MHA)**
brevifolium	B3	HQ830343	Russia, Republic of North Ossetia - Allania
brevifolium	B4	HQ830341	Russia, Republic of Tuva
caesium	**21**	**MG214799**	**Russia, Primorye Territory, Ol'khovaya Mt., 2006, *Ignatov et al. #06-2245* (MHA)**
caesium	**116**	**MG214800**	**Japan, Shikoku, 27.XI.1999, *Deguchi #204* (LE)**
caesium	141	KT580733	Russia, Amur Region
dispersum	Di 64	KT580739	USA, Alaska
dispersum	Di63	KT580738	Russia, Republic of Buryatia
dispersum	Di77	KT580740	Russia, Republic of Dagestan
drummondii	Dr73	KT580744	Russia, Murmansk Region
drummondii	Dr71	KT580743	Russia, Leningrad Region
drummondii	Dr31	KT580742	Russia, Komi Republic
flagellare	**99**	**MG214812**	**Russia, Republic of Buryatia, 18.VII.2010, *Tubanova #Kaykh-7/10* (UUH)**
flagellare	**128**	**MG214813**	**Russia, Altai, 23.VII.1991, *Ignatov #130* (MHA)**
flagellare	**183**	**MG214814**	**Russia, Kunashir Island, 05.IX.2006, *Ignatov #06-1082* (MHA)**
flagellare	**100**	**MG214815**	**Russia, Amur Region, 05.VII.2010, *Bezgodov #197* (PPU)**
flexicaule	FL212	KT580745	Russia, Republic of Buryatia
flexicaule	FL1	HQ830331	Russia, Trans-Baikal Territory
flexicaule	FL2	HQ830332	Russia, Primorye Territory
fuscescens	FU4	HQ830337	Russia, Primorye Territory
fuscescens	FU1	HQ830334	Russia, Perm Territory
fuscescens	FU2	HQ830335	Russia, Sakhalin Island
groenlandicum	122	KY296859	Russia, Murmansk Region
groenlandicum	345	KY296862	Russia, Kamchatka Territory
groenlandicum	347	KY296861	Russia, Kamchatka Territory
ignatovii	**472**	**MG214801**	**Russia, Sakhalin Island, 20.VII.2014, *Tubanova et al. #S141517* (UUH)**
ignatovii	**FD3**	**MG214802**	**Russia, Iturup Island, 11.IX.2015, *Fedosov # 15-2-123* (MW)**
ignatovii	**187**	**MG214803**	**Russia, Kunashir Island, 09.IX.2006, *Ignatov #06-3008* (MHA)**
laevidens	**L203**	**MG214804**	**Russia, Yamal-Nenets AA, 29.VII.2013, *Bezgodov #471* (PPU)**

laevidens	L86	KT580747	Russia, West Taimyr Municipal District
laevidens	L87	KT580748	Russia, Taimyr Municipal District
mayrii	**101**	**MG214816**	**Russia, Amur Region, 16.VII.2010, *Bezgodov #477* (PPU)**
mayrii	**182**	**MG214817**	**Russia, Primorye Territory, Ussuriysky Reserve, 28.IX.2006, *Ignatov, Ignatova #06-3394* (MHA)**
mayrii	**262**	**MG214818**	**Russia, Primorye Territory, Ussuriysky Reserve, 2006, *Ignatov, Ignatova #06-3400* (MHA)**
montanum	**126**	**MG214819**	**Russia, Murmansk Region, 2005, *Drugova #D3-4-91* (KPABG)**
montanum	**306**	**MG214820**	**Russia, Republic of Buryatia, 19.VII.2002, *Tubanova #13(II)* (UUH)**
montanum	**314**	**MG214821**	**Russia, Sakhalin Island, 23.VII.2014, *Tubanova, Dorzhieva #S14019* (UUH)**
muehlenbeckii	Mu62	KT580752	Russia, Republic of Buryatia
muehlenbeckii	Mu54	KT580751	Russia, Sverdlovsk Region
muehlenbeckii	Mu34	KT580749	Russia, Altai Territory
polysetum	**308**	**MG214805**	**Russia, Republic of Buryatia, 10.VII.2002, *Tubanova #3(I)* (UUH)**
polysetum	**337**	**MG214806**	**Russia, Kamchatka Territory, 11.VIII.2004, *Czernyadjeva #58* (LE)**
scoparium	**139**	**MG214807**	**Russia, Kabardino-Balkarian Republic, 30.VII.2004, *Ignatov et al. s.n.* (MHA)**
scoparium	**209**	**MG214808**	**Russia, Murmansk Region, 10.VI.2007, *Belkina #B-41-5-07* (KPABG)**
scoparium	**98**	**MG214809**	**Russia, Republic of Buryatia, 16.VII.2009, *Krivobokov #Op.21-Bar09* (UUH)**
septentrionale	S1	HQ830339	Russia, Arkhangelsk Region
septentrionale	S3	HQ830338	Russia, Kamchatka Territory
septentrionale	FIN1	KJ796546	Finland
undulatum	**142**	**MG214810**	**Russia, Republic of Buryatia, 18.VII.2010, *Tubanova #Kaykh-5/10* (UUH)**
undulatum	**143**	**MG214811**	**Russia, Kamchatka Territory, 10.VIII.2003, *Czernyadjeva #97* (LE)**
viride	1	FJ952603	Russia, Republic of Tatarstan
viride	2	FJ952602	Russia, Moscow City